

R. LIVERSIDGE

PORT ELIZABETH MUSEUM.

Distribution of birds
in relation to
vegetation

INTRODUCTION

To say that in the preparation of this paper my mind has swung back and forth in considering the possible importance of vegetation for birds, is simply to express the delightful unpredictability of bird distribution. For two points stand out from the many analyses made: The first is that a species in southern Africa so often changes its habitat from one end of its distribution to the other, that it is not necessarily safe to assume that because it is a forest bird in the south it will be a forest bird in the north. The second is that abnormal conditions such as coldness in the tropics or wetness in the south-west arid regions produce peculiarities that cloud the normal pattern of distribution.

This study of bird distribution concerns the species, not families or orders, as suggested by Winterbottom (1960) for the determination of faunal affinities. The approach here adopted is that of Chapin (1932) who states: "Each species must be studied by itself, after which it may often be included in some general scheme that will enable us to view in a *not too unnatural perspective* the wider aspects of bird distribution" (my italics). In the attempt at such an analysis, the distributions of the first 600 species numbered in Roberts (McLachlan & Liversidge 1957) have been plotted. Time prevented the entire 875 being included. It is inevitable in such a vast project to lose some detail of the finer distribution lines or extremities of distribution in the endeavour to reduce the pattern to coincide with the accompanying six maps (Figure 1). The species chosen out of the first 600 are those which have been illustrated by maps in McLachlan & Liversidge; the sea birds and those that are not common or sufficiently wide-spread have been omitted, leaving a total of 423. These 423 include non-breeding migrants many of which have distribution pattern similar to locally breeding species, though naturally these birds would not be included in faunal groupings for zoogeographic consideration.

BIRD DISTRIBUTION PATTERNS

The patterns have been separated into east, north-east, north, central-north, west/north-west and south components for convenience and because this seemed to be the only obvious grouping. Not covered in these maps are a total of 61 species found throughout southern Africa and 45 species which have an unusual distribution, but these are listed in Table 1.

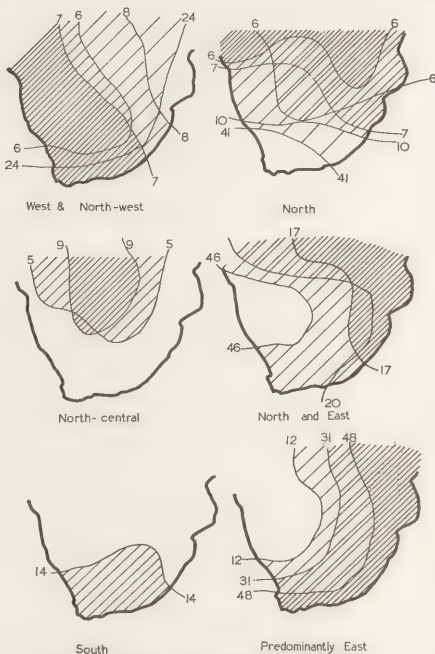


Fig. 1. Illustrating the generalised distribution patterns of South African birds. Each map has marked the number of species that occur on the line of limit of each pattern.

DISTRIBUTION OF BIRDS IN RELATION TO VEGETATION

TABLE 1

Area	No. of Birds	Percentage of No. Mapped of 423	Percentage of Total considered 600
Uncommon or very restricted	177	—	30
Whole Union ..	61	14	10
Specialized and restricted	45	11	7½
Predominantly east ..	91	21	15
North and east ..	83	20	14
North-central ..	14	3	2
North	70	17	11
West/north-west ..	45	11	7½
South	14	3	2
Total	423	100	99

The group of 45 species with distinctive patterns could perhaps be reduced in number with more detailed knowledge and unfortunately it is from this group that many false impressions are gained. It can be seen that the east and north-east components have between them 41% of species and thus more than any other section. Many species unmapped would probably fall into this group since they include the southern extension (down the east coast) of many so-called tropical species. Thus the most important and varied group of bird species are those of south-east Africa; they are numerically greater than those found in the south-west (arid) regions.

The many finer points which unfortunately have been omitted in the generalized maps are more important from the vegetational point of view. Thus we find many limits of bird distribution which fit the finer vegetation types mentioned below. This does not only apply to our own regions as the following quotation from Hall (1960), who refers to Angola, indicates: "Repeatedly it will be found that birds of many different families have similar specific or subspecific ranges which lie along the same boundaries and co-incide with the limits of one or another type of vegetation". Some of the commoner minor limits of distribution are mentioned and illustrated later.

VEGETATIONAL DISTRIBUTION

In birds there are only two sources of mapped distributions in Southern Africa (McLachlan & Liversidge 1957, Skead 1960) apart from detailed taxonomic papers on individual species. Plants however, have received a variety of cartographical representations

ranging from the generalized C.C.T.A. map (Keay 1959), suggested for this conference, to the very detailed veld-types published by Acocks (1953). Two South African botanists whose work appears largely to have been overlooked and yet whose maps are most useful from the ornithologist's point of view are Adamson (1938) and Pole-Evans (1936). For example both show a tongue of a vegetation-type north from Kuruman which co-incides with the limits of distribution of several lark races. In the confusion of the detail of Acocks (1953) this region is not apparent. There seems to be some disagreement on whether the Kalahari thornveld should be included in southern savanna or not. From our point of view it is rather a large important tract of land. If "life-form" has any importance in vegetation types, then it would seem right to include the Kalahari in the savanna as most South African botanists have done. "Life-form" refers to the general appearance, size, foliage, etc., that a plant assumes under local ecological conditions. The author prefers the use of Pole-Evans map for the ecological aspects of animal distribution but Keay's map has been used as the recommended map for this conference.

FACTORS INFLUENCING DISTRIBUTION OF VEGETATION

Adamson (1938) considers that the broader vegetational zones such as forest and savanna are influenced by climate. The lesser vegetation-types are influenced by climatic, physiographic, edaphic, biotic and historical factors. On the smaller divisions there is argument whether climatic or edaphic factors are dominant in their influence over the vegetation. It would appear at least in the eastern Cape that edaphic factors are more important as the following example shows. The typically "Cape" vegetation extends east to Port Elizabeth; there are, however, patches in the Alexandria division and in the Port St. John division which grow on outcrops of the "Cape" geological system in these two areas, though the climate and the surrounding vegetation is of a more subtropical nature and certainly not a winter rainfall area.

Of the climatic factors the rainfall is the most important. This can be seen from the general similarity between the patterns of the mean average rainfall map and the vegetation map. The temperature appears to have a completely independent pattern, associated with altitude but, except along the low-lying east coast, showing no clear agreement over the rest of the country. Frost patterns agree roughly with the isotherms.

COMPARISON OF PLANT AND BIRD DISTRIBUTIONS

Using the broad zones of the C.C.T.A. map, there are 11 species of birds which have a distribution similar to that of the southern savanna and nine which conform to the same veld-type if the Kalahari thornveld is included (Table 2). Two species conform roughly to the south-west arid region, viz. Stark's Lark *Spizocorys starki* and Red-eyed Bulbul *Pycnonotus nigricans*. Three species agree with the south-west Cape, namely Victorin's Scrub-Warbler *Bradypterus victorini*, Orange-breasted Sunbird *Anthobaphes violacea* and the Cape Sugarbird *Promerops cafer*.

There appears to be little correlation between bird distributions at the species level and vegetation types. However, as already mentioned the boundaries of the two very often co-incide along part of their limits of occurrence. The difficulty appears to be largely due to the variability of birds' habits. As Winterbottom (1959) states with regard to certain species "although characteristically or exclusively forest birds in the south, further north they become birds of the savanna woodlands and are often absent from true forests". This argument may be applied in reverse and not confined to forest and savanna alone. It is not surprising therefore that the birds do not fit in with single vegetation-types. Despite this discrepancy in detail we need look no further than the same article by Winterbottom to

TABLE 2
BIRDS OF THE SAVANNA

Excluding Kalahari-thornveld

White-faced Duck	<i>Dendrocygna viduata</i>	..	..	..	..	..	(100)
Brown snake-eagle	<i>Circus cinereus</i>	..	..	..	..	..	(145)
Little Sparrowhawk	<i>Accipiter minullus</i>	..	..	..	..	..	(158)
Crowned Crane	<i>Balearica regulorum</i>	..	..	..	..	..	(214)
Emerald-spotted Dove	<i>Turtur chalcophilus</i>	..	..	..	..	..	(321)
Green Pigeon	<i>Treron calva</i>	..	..	..	..	..	(323)
Black Cuckoo	<i>Cuculus cafer</i>	..	..	..	..	..	(344)
Great Spotted Cuckoo	<i>Clamator glandarius</i>	..	..	..	..	..	(346)
Lesser Honeyguide	<i>Indicator minor</i>	..	..	..	..	..	(442)
Golden Oriole	<i>Oriolus oriolus</i>	..	..	..	..	..	(519)
White-browed Scrub Robin	<i>Erythropgia leucophrys</i>	..	..	..	..	..	(588)

Including Kalahari-thornveld

White bellied Stork	<i>Sphenorhynchus abdumii</i>	..	..	..	..	..	(78)
Pallid Harrier	<i>Circus macrourus</i>	..	..	..	..	..	(168)
Montagu's Harrier	<i>Circus pygargus</i>	..	..	..	..	..	(170)
Harlequin Quail	<i>Coturnix delegorguei</i>	..	..	..	..	..	(190)
Lesser Gallinule	<i>Porphyrio alleni</i>	..	..	..	..	..	(209)
Wattled Crane	<i>Bucconas carunculatus</i>	..	..	..	..	..	(215)
Bronze-winged Courser	<i>Rhinoptilus chalcopterus</i>	..	..	..	..	..	(280)
Cuckoo	<i>Cuculus canorus</i>	..	..	..	..	..	(340)
Scops Owl	<i>Otus scops</i>	..	..	..	..	..	(363)

realize that his three avifaunal divisions are in actual fact coincident with vegetational divisions, called by him "winter-rainfall area, temperate forest and karroo". The winter rainfall area is typically Cape vegetation.

Chapin (1932) says bird dispersal in the Congo is determined by climate which acts upon birds through the vegetation "save perhaps the cold of the mountains". In an earlier paper (Liversidge 1959) I came to the conclusion that temperature was the principal restricting factor for species of tropical montane forests. It is evident now on further analysis that this is due to the extreme conditions within the tropics since, in the southern ranges of these montane species, temperature appears to play no part and they occur on the much hotter Karoo plains. Winterbottom (1959) also noted a change in habitat of Karoo species which extend into the winter-rainfall area. Hall (1960) remarks upon the same thing in Angola with regards to birds of the plains when they occur in the mountains. Not only is there a variation of habitat, often at the limit of a bird's distribution, but there is often a change of status from resident and local over most of the range to being a bird of definite migratory behaviour.

Individual plant species or types are often associated with a bird's distribution. The palms for example of the genera *Elais* and *Rhaphia* are associated with the major portion of the distribution of the Palm-nut or Egyptian vulture *Gypohierax angolensis*. The Palm swift *Cypsiurus parvus* occurs where it can nest and roost amongst palms though it is interesting to note it has recently taken to breeding upon bridges. However, here again there are multiple factors involved. In Rhodesia for example the Streaky-headed Seed-eater *Poliospiza gularis* occurs strictly in *Brachystegia* woodlands (Liversidge 1959) but in the eastern

Cape no such woodland exists and the same bird occurs in totally different scrub vegetation. Another species which is associated with a particular plant, namely the Sword Plant *Sansevieria*, is the Spectacled Weaver *Hyphantornis ocularius* which uses fibres stripped from the leaves for its nest. This association is quite marked in the eastern Cape where the weaver nests in the veld away from water. To the north the Spectacled Weaver is associated with water and this factor is probably responsible for its absence in northern Bechuanaland where a belt of *Sansevieria* occurs from Maun towards the east.

Associations between plant and bird species are evidently long established since morphological adaptation has occurred in some species. Irwin (1959) shows that what was considered to be a single species, the Black Tit *Parus niger* actually has two forms, one of which occurs on the western part of the range and is associated with *Acacia* woodland; and the other, a heavier billed bird, occurs in *Brachystegia* woodland. Where islands of one type of vegetation are found within the other, populations of the expected form of Black Tit are always present.

DISCUSSION

From the evidence here adduced, bird distribution seems to be closely associated with vegetation but the vegetation-types, as such, show little agreement with bird distribution patterns. It is therefore unlikely that vegetation, considered from a botanical point of view, is in itself of major importance. "Life-form" is probably of some importance. For example, some predators obviously require perches which give a suitable vantage point in order to spot their quarry. Further many birds are dependent upon flowers or fruits as a source of food. For example, various sunbirds (Nectariniidae) are attracted to different vegetation types depending upon the flowering of suitable plants. The full details are uncharted, but in June and July aloes flower at Addo; in August and September, the kaffirboom *Erythrina caffra* flowers at Alexandria; and in January and February *Brunsvigia* flowers along the coastal dune. Sunbird populations which are noticeably larger than normal occur in these areas at the times given. Aloes, however, may flower in different parts of their range at different times, as much as four months apart over a distance of 150 miles (as from Port Elizabeth to Amatola Mountains). Yet it seems more likely, though we have no facts as yet, that individual sunbirds do not follow the successive flowering of a given plant in adjacent districts but remain in the same broad area and change their food plants. The Knysna Lourie *Turacus corythaix* remains, on the whole, localized but shows definite seasonal movements within its habitat according to the ripening of the various species of fruit it eats.

Thus while vegetation may influence the distribution of some species locally, it is not the main factor with which we may associate bird distribution. There must be some factor influencing both. A brief inspection of the climatic factors indicates that the rainfall patterns agree most closely with bird and plant distribution patterns. This is in agreement with Chapin. However, Poynton (1961) shows the "Tropical" east coast element is possibly associated with a minimum temperature range. This can only be true of the warmer areas since mean absolute minimum temperature patterns show no correlation with bird patterns except for the warmer isotherms. This presents the possibility that geographically the factors influencing bird distribution vary; thus within dry areas, rainfall is important; in warmer areas isotherms are important. *Dominant climatic factors in a region influence the birds of that area* and where these dominant climatic factors vary, from region to region, the main factors influencing bird distribution of these regions also vary.

If this variability of factors influencing bird distribution is accepted then it is easy to understand how the different concepts in avian distribution fail.

Ornithologists tackle the problem of geographical distribution in three ways. Firstly there are the so called "life-zones", zoogeographical regions based primarily upon isotherms.



Fig. 2. The biotic provinces of Southern Africa as suggested by McLachlan and Liversidge.

These life-zones have become the classical units of broader zoogeography and the original zones, such as the Ethiopian Region proposed by Sclater, are generally accepted today. The second concept is that of *biomes*, mainly supported by the American ecologists and formulated upon natural areas based upon so called climax vegetation. Unfortunately from the mapping point of view, *biomes* do not form continuous areas. This gave rise to the third concept, the so-called *biotic provinces*, which in fact amount to an attempt to couple *biomes* to geographical distributions by making continuous uniform units. Biotic provinces while not being highly satisfactory are in general use throughout the world.

The biotic provinces for southern Africa have been published (McLachlan & Liversidge 1957, and Winterbottom 1960) (Fig. 2). In practice distribution of birds does not fit satisfactorily into biotic provinces, though many species share boundaries similar to those illustrated. The names and areas applied to the biotic provinces, however, are in common use.

These biotic provinces cut across major climatic regions. The subdivisions proposed by Winterbottom (1960) for the western Cape are in agreement with these findings. For the Transvaal highveld and lowveld, it would seem more satisfactory to revert to the "forest" fauna and "steppe" fauna divisions suggested by Reichenow rather than western and eastern designation as commonly used (Chapin 1932).

Before any conclusions can be drawn about the bird faunal units of the area between the Zambezi and Vaal systems it is obvious that a much more detailed knowledge of the dispersal of birds up to the south equatorial divide is needed. In fact a picture of the whole Ethiopian region seems essential and with the checklists and books recently published it should be possible to make such an analysis.

SUMMARY

Analysis is made of distribution patterns of 423 species which fall into the divisions east, north-east, central, west-north-west and south. Vegetation maps and factors influencing vegetational distributions are discussed. Plant and bird distribution is compared; there is only a poor correlation of broad zones, but a close matching of boundaries with vegetation types in many cases. Individual species are influenced by certain types or species of plants. It is concluded that dominant climatic factors influence bird distribution and where such factors change the dominant factors influencing bird distribution also change. The concepts of life-zones, biomes and biotic provinces are discussed.

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DISCUSSION

Prof. van Zinderen Bakker: In these discussions there has been a tendency to consider the influence of single factors separately, but this procedure may mislead. We are dealing with living organisms for whom such matters as climate, soil, vegetation and temperature form an interacting complex.

Mr. Liversidge: I agree, and think that Dr. Poynton, for instance, gave too much emphasis to the effects of temperature. However, I felt that vegetation represented one end-point of the "interacting complex", and thus expected to find some coincidence with avian distribution, but did not.

Prof. van Zinderen Bakker: Temperature is probably the primary factor, influencing all others when it changes.

Dr. Poynton: I certainly do not regard temperature as the only factor determining distribution and agree with Mr. Liversidge that rainfall is limiting in the west. However, in regions where rainfall is not limiting and where ecological conditions are generally constant, temperature effects distribution. It acts directly and not indirectly as does precipitation. In this, it is important to consider the distribution of major systematic groups rather than of individual species.

Prof. Ewer: I am disturbed by this "lumping" tendency. The things which will effect distribution, especially amongst birds which are free of so many limitations, must be closely related to the individual species' way of life. Black-headed Gulls in England, for example, have become inland birds, changing their distribution completely, following a change in habits. It seems a doubtfully valid procedure to throw all species in a group together and expect a meaningful result to emerge; and I become increasingly sceptical regarding the significance of attempts to reconstruct a phylogenetic zoogeographical picture. We are forgetting how competition may affect distribution and that speciation may be in active progress. We are dealing not with static things, such as so many cities or mountains, but with living organisms.